

ORIGINAL ARTICLE

Running title: Social learning via video screens

Social learning in nest-building birds watching live-streaming video demonstrators

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/1749-4877.12316](https://doi.org/10.1111/1749-4877.12316).

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Abstract: Determining the role that social learning plays in construction behaviours, such as nest building or tool manufacture, could be improved if more experimental control could be gained over the exact public information that is provided by the demonstrator, to the observing individual. Using video playback allows the experimenter to choose what information is provided, but will only be useful in determining the role of social learning if observers attend to, and learn from, videos in a manner that is similar to live demonstration. The goal of the current experiment was to test whether live-streamed video presentations of nest building by zebra finches *Taeniopygia guttata* would lead observers to copy the material choice demonstrated to them. Here, males that had not previously built a nest were given an initial preference test between materials of two colours. Those observers then watched live-stream footage of a familiar demonstrator building a nest with material of the colour that the observer did not prefer. After this experience, observers were given the chance to build a nest with materials of the two colours. Although two-thirds of the observer males preferred material of the demonstrated colour after viewing the demonstrator build a nest with material of that colour more than they had previously, their preference for the demonstrated material was not as strong as that of observers that had viewed live demonstrator builders in a previous experiment. Our results suggest researchers should proceed with caution before using video demonstration in tests of social learning.

Keywords: Construction behaviour, Copying, Nest, Social learning, Video playback, Zebra finch

Introduction

Learning that is influenced by observation of, or interactions with, another individual (social learning *sensu* Heyes, 1994) occurs across a wide range of taxa including insects, birds, reptiles and mammals (Avarguès-Weber et al., 2013; Kis et al., 2015). Perhaps owing to its ubiquity, social learning has become a well-documented phenomenon (Hoppitt and Laland, 2013). For decades now, studies have focused on *what* observing animals may learn from a demonstrator. For instance, the observer may learn that food is available at a location where they have seen a demonstrator previously feed (local enhancement; Webster and Laland, 2013). Or, the observer may learn to interact with a certain object at a particular location, to obtain food, after watching a demonstrator do so (stimulus and local enhancement, respectively; Guillette et al., 2014).

One method for examining the mechanistic basis of social learning, beyond local and stimulus enhancement is the two-object/two-action test. Here, one group of observers watches a demonstrator gain an outcome by performing one action (e.g. by pushing or using the beak), while a second group of observers watch the demonstrator gain an outcome by performing a different action (e.g. by pulling or using the foot) directed at one of two (or more) options (stimuli). Importantly, when the observer is given the chance to interact with the test box, either action, not just the action used by the demonstrator, is sufficient to produce the outcome. Budgerigars *Melopsittacus undulates* that watched a demonstrator either pull or push a stopper to gain entrance to a box to receive a food reward copied the specific action used by the demonstrator. These observers, moreover, were more likely to direct whatever particular action they observed, towards the object (the stopper in this case) that matched the colour and location of the object that was manipulated by their demonstrator (Heyes and Saggerson, 2002). This example illustrates what observing animals may learn from watching demonstrators overcome an obstacle to obtain food. But this methodology

may not be sufficiently refined to determine what observing animals learn about construction behaviour (e.g. building a nest or making a tool). This is because nest building and tool making often require multiple steps (e.g. acquiring material, manipulating and/or processing material, acquiring additional material; Guillette and Healy, 2015; Hansell and Ruxton, 2008; Healy et al., 2008; Klump et al., 2015) and are longer in duration relative to one-time problem-solving tasks (e.g., moving a door or removing a stopper to obtain food). Nest building may also be more open-ended than are one-time problem solving tasks because there are multiple ways (e.g. different behaviours, steps, movements, etc.) to achieve the same or a similar final nest structure (Bailey et al., 2015; Breen et al., 2016; Guillette and Healy, 2015; Muth and Healy, 2014).

To study the role of social learning in construction behaviour may then require the ability to manipulate many (often subtle) components of the demonstrator's behaviour in order to confirm their impact on the observer, a feat made possible using video presentations. Unlike live demonstrators, video demonstrators can allow for precise control (or experimental manipulation) of the public information to which the observer is exposed. Importantly, video demonstrations not only enables standardization of the demonstration in social learning trials, which can result in increased repeatability through control of the stimulus but may also reduce the time to complete testing, the number of animals (an ethical advantage) and overall costs (Oliveira et al., 2000). On the other hand, the drawbacks of using video demonstration in social learning experiments could be that the observing animals may not respond to/learn from video stimuli or do so in a way that is different from viewing live conspecifics (D'Eath, 1998).

There are a growing number of studies showing that video stimuli will elicit natural behaviour across a range of species: chimpanzees *Pan troglodytes* (Campbell and de Waal, 2011); hens *Gallus domesticus*, (Evans and Marler, 1991); budgerigars *Melopsittacus*

undulates (Gallup et al., 2015); Bengalese finches *Lonchura striata* (Ikebuchi and Okanoya, 1999); Jacky dragons *Amphibolurus muricatus* (Ord et al., 2002); gloomy octopus *Octopus tetricus* (Pronk et al., 2010). Female Japanese quail *Coturnix japonica*, moreover, can transfer individual recognition of conspecific males from a video playback to a live animal (Ophir and Galef, 2003). But eliciting natural behaviour is not the same as eliciting behaviour to the same degree as would be observed if the observer was watching a real (i.e. live) demonstrator. In the few studies that have made direct comparisons between live and video presentations the responses of observers have ranged from no difference (e.g. Evans and Marler, 1991), through an attenuated response to video stimuli (e.g. Ikebuchi and Okanoya, 1999) to, perhaps most surprisingly, an enhanced response (Swaddle et al., 2006).

Given the variety in the levels of behavioural response to the two kinds of presentations (live and video) of conspecifics, it is possible that observer animals pay attention to different information in video presentations of demonstrators than they do to the information provided by live demonstrators. Alternatively, but not mutually exclusively, it is possible that observers simply pay more or less attention to video presentations altogether. If video presentations do not always have the same absolute impact as do live demonstrations, then the value of video presentation might have to be used with caution. For example, when different groups of Burmese red jungle fowl *Gallus gallus domesticus* observers watched live demonstrators, video demonstrators with the sound turned off, or video demonstrators with sound, they copied the foraging choices of the live demonstrators and the video demonstrators with sound. That is, observers did not copy if they could not hear the demonstrators (McQuoid and Galef, 1993, 1992). And yet, zebra finches *Taeniopygia guttata* copied silent video playback but failed to copy when the video demonstration was played back with sound (Guillette et al., 2014; Guillette and Healy, 2017). This suggests that non-interactive vocalizations can disrupt public information use in zebra finches, but such

vocalizations do not have this impact on fowl. The disruption in public information use for zebra finches is not regulated by vocal learning ability *per se* (zebra finches are vocal learners and fowl are not) because budgerigars, who are also vocal learners, will copy the action of video demonstrators in a two-action, two-object test when the videos are played back with sound (Heyes and Saggerson, 2002; Mottley and Heyes, 2003). These studies highlight the need to test for correspondence between observers' responses to live versus video demonstrators.

In zebra finches, females will copy males demonstrating novel food choices, both live and on video. Male zebra finches do not copy demonstrators of either sex, when the task involves foraging (Guillette et al., 2014; Guillette and Healy, 2017, 2014). The behaviour in which we wish to examine the role of social learning, however, is that of nest building, a behaviour performed almost entirely by males in this species. Therefore, the goal of the current experiment was to test whether video demonstrators have the same effect on nest building by male observers as do live demonstrators. Specifically that when they build their first nest, adult male zebra finches with no building experience, copy the material choices of familiar conspecifics (Guillette et al., 2016). To do this we live-streamed zebra finch male demonstrators building a nest to observers watching on a thin-film-transistor (TFT) screen. These screens have constant illumination and can accommodate the higher flicker-fusion frequency of avian visual systems (Galoch and Bischof, 2007; Ikebuchi and Okanoya, 1999; Ophir and Galef, 2003). In the current study the demonstrator was in the same room, but was visually occluded from the observers, so that the observers and the demonstrators could vocally interact, but all visual information (i.e. the material with which to build a nest) available to the observer was provided via the screen. If video presentations are to be useful as a methodology for investigating the role that social learning may play in the acquisition of

construction behaviour, then the live-streaming video demonstration should result in males copying the nest material used by familiar demonstrators (Guillette et al., 2016).

Materials and Methods

Subjects

All subjects (43 of each sex) were bred at the University of St Andrews, UK. After becoming nutritionally independent (35-40 days post-hatch) birds were housed in cages of same-sex individuals (~30 individuals per cage, 140 × 71 × 122 cm) and kept at ~20°C with relative humidity ~50% and 14:10 light: dark cycle. Birds were given *ad libitum* mixed seeds, water (vitamin supplemented 3 × per week), cuttle bone, oystershell, vitamin block and fresh spinach (3 × per week). The floors were covered with pressed wood pellets and there were several perches of different diameters. Birds were visually assessed for health at least two times per day by the animal care staff. At the end of the experiment birds were returned to these group-housing cages. All birds were sexually mature adults (>90 days post-hatch) at the time of testing.

The work described here was conducted with the approval of the University of St Andrews Animal Welfare and Ethics Committee.

Apparatus

The experimental trials were carried out in a test room that contained one demonstrator cage and four observer cages. White opaque curtains hung between each cage and allowed for vocal, but not visual contact between the different cages. Each cage (100 × 50 × 50 cm)

contained two water and two food bowls, six perches, cuttlefish bone, oystershells and vitamin block that remained available to the birds throughout the experimental trial. A video screen (ViewSonic Thin Film Transistor, model #VS15804, screen dimensions $61.5\text{ l} \times 34\text{ h}$ cm) was situated 15 cm from the long side of each observer cage and was concealed by a white opaque curtain. The demonstrator cage was identical to that of the observers'. Each cage contained three bird box cameras (SpyCamera CCTV, Bristol, UK) connected to a laptop computer to record the behaviour of the birds. A GoPro Hero3 (GoPro, Incorporated, USA) located outside of the demonstrator's cage was used to live stream the behaviour of the demonstrator to the observers. The mini-HDMI connection from the GoPro was connected to a 1×4 HDMI splitter (HDelity by Cabbleson), which connected to each of the four monitors located outside each of the four observer cages via a separate HDMI cable. Using this experimental set up four observer pairs were tested in each trial (four observers per one demonstrator).

Procedure

We selected non-related male-female pairs and housed them in a cage ($100 \times 50 \times 50$ cm) in a room that was separate from the colony room cages, and the experimental cages. Pairs were also moved to this room between the phases of the experiment (i.e. the initial preference and observation – described below). The observer birds had no previous experience of nest building and had not been used previously in any other behavioural experiment. Observers were paired for at least six days prior to testing to allow for pair-bond formation. All demonstrator birds had previous experience with building a nest. Additionally, before they were used as demonstrators in the current experiment, each demonstrator pair had to begin building a nest with 100 pieces of string (same number of pieces used in Guillette et al. 2016,

which is approximately 25% of a complete nest: Bailey et al., 2014). The observer pairs were not able to see the demonstrator pairs build this nest. All observers and demonstrators were familiar with one another because they were housed in the same colony room cages for several months prior to the experiment. Each observer pair was run in one trial, but several demonstrator pairs were used in more than one trial (6 demonstrator pairs were used in one trial each, 1 pair was used in 2 trials, 1 pair was used in 3 trials). There were 35 observer and eight demonstrator pairs.

Observer initial material preference

The male in each observer pair (it is the male that is the primary builder in zebra finches) was tested for his initial preference for either of two different colours of string (pink and orange, James Lever Jute Craft Twine, Bolton, UK; hereafter referred to as *material*) that were to be used in the subsequent experimental phases.

Four observer pairs were moved into each of the observer experimental cages in the test room the day before the initial material preference test (Figure 1). One-hour after lights-on we gave each observer 25 pieces of pink material (each 15 cm long) and 25 pieces of orange material. Each piece of material was tied to the front of the observers' cage. This allowed the observer to interact with the material, but not to carry it away or to build a nest.

We recorded the behaviour of the observers for four hours, after which we removed all material from the observers' cage and immediately scored the video to determine the amount of time that each observer male interacted with the material of each colour. If the male had spent less than 60 seconds interacting with the material, the pair was run in another four-hour preference test the next morning. Each male's material preference was calculated by dividing the amount of time he spent with the material that he interacted with the most by

the total amount of time he spent interacting with both colours of material. The maximum time allowed for the initial material preference was eight hours. As three observer males had no initial colour preference and the video failed during one initial material preference test, these four pairs did not proceed to the rest of the experiment. The average time these birds spent interacting with the tied-down string was 1590.91 ± 1298.59 seconds, range was 144.5 to 4205.5 seconds.

Demonstrator pre-observation building

This phase started as soon as there were four observers with the same initial material preference. We gave the demonstrators 100 pieces (15 cm each) of the observer male's least preferred material. These 100 pieces were placed against one of the side walls of the demonstrator's cage, and sham tied to the cage. These sham-tied pieces were placed such that they were touching the white string that had been tied to the cage side wall. Tied to the opposite cage wall were 50 pieces of string of the observers' initially preferred material. Because they were tied to the cage wall, the demonstrator could not build with these pieces of string. In this way, the demonstrators could interact with both, but only build with the observers' least preferred material. We hung a wooden nest cup ($11 \times 12 \times 4.5$ cm) on the long wall of the demonstrator's cage (Figure 1). This phase continued until the demonstrator male had taken all 100 pieces to the nest cup (mean \pm standard deviation: 1005 ± 1074 min; range = 400 to 3713 min). The purpose of this phase was to ensure that the demonstrator was engaged in nest building before the *observation* phase began. This phase was not broadcast to the observers.

Observation

The observation phase began after the demonstrator had placed all 100 pieces of the observers' initially unpreferred material into the nest box. The 50 pieces of the observers' initially preferred material remained in the demonstrator cage tied to the side wall. The demonstrators then received 50 additional pieces of the observers' initially unpreferred material. The behaviour of the demonstrators was then live-streamed and broadcast to each of the monitors on each of the four cages containing the observer pairs in the experimental room. The *test phase* continued until the demonstrator male had added all 50 additional pieces of material to the nest (see Guillette et al., 2016 and Figure 2b for pictures of pink and orange nests built with 150 pieces of material). By having both materials (both the unpreferred and preferred) present during the *observation* phase we can attribute a change in preference to the demonstrated material during the *test* phase as a result of social demonstration, rather than due to exposure to the demonstrated material.

Test phase

This phase began as soon as the *observation* phase was complete. First, we ceased live streaming the demonstrator's behaviour to the observers via the monitor. We then gave each observer a nest cup and 25 pieces of pink and 25 pieces of orange material (15 cm each, see Figure 1). The placement of each coloured material on the floor of the cage mirrored that that had occurred in the demonstrator cages. This experimental design does not allow us to distinguish if the observer in fact copied the *colour* or *location* from which the demonstrated material was taken. Rather than the type of information we were simply interested in any copying by the observer of the behaviour of the demonstrator with respect to which material was used to build the nest. The *test* phase ended once all the material had been placed into the

nest cup. We assessed the *final material preference* of an observer as the proportion of material of the first 25 pieces he had deposited into his nest that were of the demonstrated material. This score was therefore near to 1 if the observer did not use the material he initially preferred but instead built with the demonstrated material, the score was near 0.5 if the male incorporated equal number of pieces of his initially preferred and the demonstrated material, and the score was 0 if the male built his nest with 25 pieces of his initially preferred material.

Statistical analyses

Testing for copying by observers that watched a live-streamed demonstrator via a video screen

We conducted a one-sample Wilcoxon signed-rank test with the chance level of 0.5 (no preference or using both materials equally) for the *initial material preference* and *test* (final material preference). We report the mean proportion and the 95% confidence intervals. We also used a related-samples Wilcoxon test to test for a change in material preference between the *initial material preference* and final material preference in the *test* phase. Two pairs did not build in the *test* phase, the video failed during the *test* phase for two additional pairs and the female built the majority of the nest for three additional pairs. The final number of observer pairs analysed was therefore 24.

Comparison with data from birds watching a live demonstrator (Guillette et al. 2016)

We used an independent samples Mann–Whitney U-test to test for differences between the two groups in their final preference test. Group 1 consisted of the observers in the current experiment that watched a live-streamed demonstrator via a video screen and Group 2

consisted of observers from Guillette et al. (2016) that watched a live demonstrator build a nest.

Results

In the initial material preference test males preferred the non-demonstrated material to the demonstrated material (One-sample Wilcoxon test: $W = -4.11$, $n = 24$, $p < 0.001$) but they had no preference in the final preference test (One-sample Wilcoxon test: $W = -0.19$, $n = 24$, $p = 0.85$).

After observing a demonstrator build with material of his unpreferred material, sixteen (of 24) males' preference for the demonstrated material increased. The preference of seven males for the demonstrated material decreased after the *observation* phase, and one male did not change his preference for the demonstrated material (see Figure 3 for the initial and final material preference, for each of the 24 males). For all males combined, preference for the demonstrated material increased from the initial (0.25 ± 0.07) to the final material preference test (0.49 ± 0.14 ; related-sample Wilcoxon test: $W = 2.75$, $n = 24$, $p = 0.006$). Observer males in the familiar treatment group from Guillette et al. (2016; 0.85 ± 0.19) had higher final preference scores than did the observer males in the current experiment (independent-samples Mann-Whitney U test: $U = 34.5$, $n = 32$, $p = 0.006$, see Figure 4 for the initial and final material preferences of birds in the current experiment as well as those from Guillette et al. (2016)).

Discussion

After watching a live-streaming video of a familiar male demonstrator building a nest with a material that the observer did not initially prefer, the observer was given material of two colours with which to build his first nest. The colour/location of one of the materials matched that used by the demonstrator, and the other material was of the colour/location that the observer had initially preferred. For two-thirds of the observers', preference for the material used by the demonstrator increased from the initial to the final material preference test. While these results were qualitatively similar to data from live demonstrators (Guillette et al., 2016), the strength (or quantity) of copying was much less: birds viewing live demonstrators had a stronger preference for the demonstrated nest material having viewed a familiar male build a nest with that material, relative to birds that viewed the demonstrator building on a live-streamed video screen.

These data differ, then, to the effects of live or video demonstrators on foraging choices by observing female zebra finches, where there seemed to be no qualitative or quantitative difference in social learning dependent on the visual format (Guillette et al., 2014; Guillette and Healy, 2017). With the current set of results we cannot differentiate between two possible explanations for the variation in the effectiveness of video demonstration: 1) the sex of the observer i.e. only female zebra finches copy from videos and males do not, or, 2) the behavioural context i.e. foraging versus nest building (Guillette et al., 2016; Guillette and Healy, 2017).

It is unclear why learning should vary according to the presentation of live versus video demonstrators. The first hurdle to using video demonstration in place of live demonstration is to gauge that the observers are attending to the video information. Indeed, a recent study using video playback of blue tits (*Cyanistes caeruleus*) consuming food showed that observing individuals faced the video screen more often when the video demonstrator was eating aversive versus palatable food but that did not translate into the majority of

individuals using this public information to avoid aversive food (Hämäläinen et al., 2017).

While many studies provide evidence that animals pay attention to and show a behavioural (e.g., Hernandez and MacDougall-Shackleton, 2004) or neuronal response (Avey et al., 2005) to conspecifics when they are presented on video screens, the current results suggest that the way this information is processed and then used in later decisions differs according to the mode of presentation. Another example with (potentially) surprising results is a study that compared the ability of chimpanzees (*Pan troglodytes*) and young children (*Homo sapiens*) to use either a video or live demonstration to guide their search for a hidden object. The children found fewer objects after the video presentations than they found after the live presentations. The chimps, on the other hand, performed well regardless of the means by which they viewed the demonstrators (Poss and Rochat, 2003). Like the zebra finches, the children learned socially from live conspecifics, but failed to use that same information, in the same context, when the information was provided via a video.

Some animals will learn to manipulate/modify objects successfully without viewing a live demonstrator (Price et al., 2009). For example, chimps that watched tool construction and successful retrieval of a food reward were subsequently able to construct a tool and retrieve a food reward with that tool. However, seeing the tool construction was not necessary for success: chimps that saw only the tool being used, but did not see any construction behaviour, could also construct and use the tool. These results, combined with our finding that zebra finches use public information when making decisions about nest material selection, suggest that video demonstration is a tool for asking questions about the role that social learning plays in physical cognitive abilities (i.e. manipulating, handling, and modifying material) that requires further investigation.

Such an investigation might begin with a comparison of the effects of video play back varying in social interaction (similar to Guillette and Healy 2017 in a foraging context) needs

to be undertaken. Similarly, it may be possible to use video presentations of different motor patterns (e.g. holding the material from the middle or end) to achieve the same end (goal) can be played to observers to test for imitation learning about physical cognition (e.g. in nest building; Guillette and Healy, 2015), which is thought to be one of the hallmarks of cumulative cultural evolution (Dean et al., 2012).

Because we saw an increased preference for the demonstrated material in only two thirds of the birds, however, we would recommend that future experiments designed to test the mechanisms the role of social learning in construction behaviour should first use both highly trained live demonstrators as well as videos of these demonstrators. Only if correspondence between performances of the observer using both presentation modes is established will it be useful then to use video presentations.

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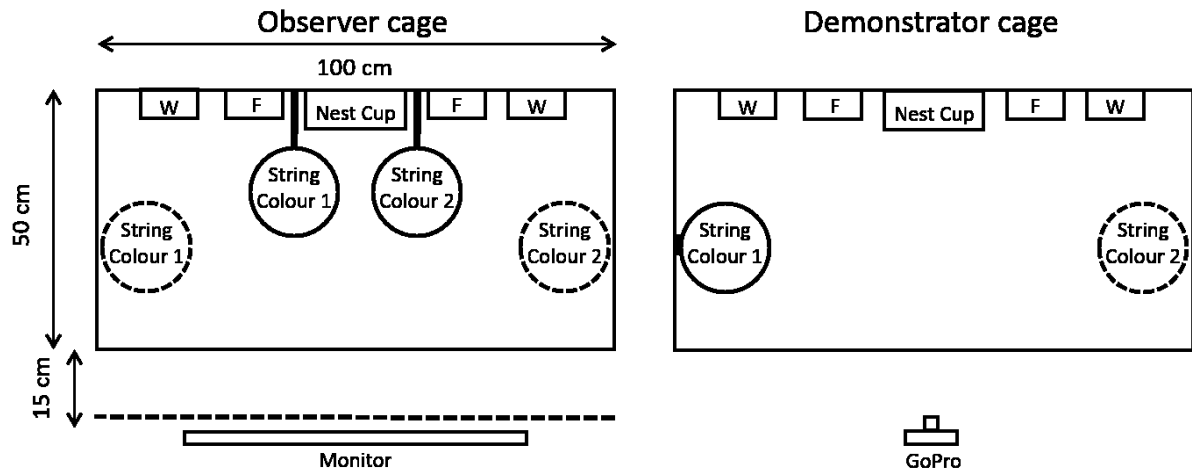


Figure 1 Schematic top-down view of the experimental cages. W = water dish, F = food dish. The observer cage is pictured on the left. Although the cages are pictured as next to each other the observers could see the demonstrators only via the monitor (when the monitor was available). A solid line around the string represents string that was tied down to the cage and could therefore not be carried around or used to build a nest. The dashed line around the material represents string that was not tied down (i.e. it was loose) and could therefore be used to build a nest. The figure here represents all phases of the experiment. In the *initial preference test* the observer was given 25 pieces of pink and 25 pieces of orange material that were tied to front wall of the cage. In the *pre-observation phase* the demonstrators were given a nest cup and 50 pieces of the observer males' preferred material that was tied to the wall of the cage (material 1) and 100 loose pieces of the observer males' least preferred colour/location (material 2). In the *observation phase* the demonstrator was given an additional 50 pieces of the observer males least preferred material to continue building a nest with and this behaviour was live streamed to the observers on the monitor. In the *test phase* the observer was given 25 pieces of each material and a nest cup.



Figure 2 Photograph of representative demonstrator nests built with 150 pieces of orange or 150 pieces of pink material. Each piece of material was 15 cm long.

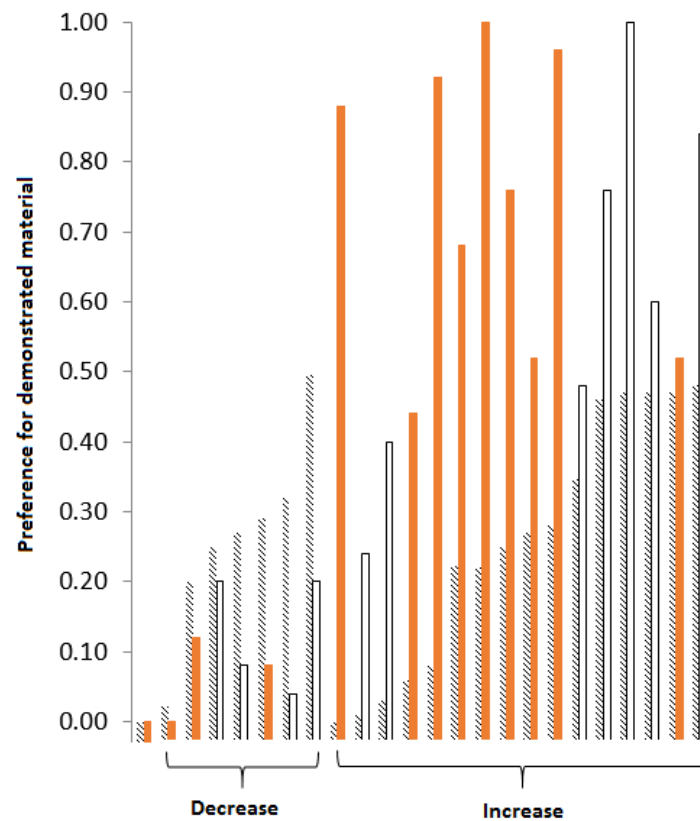


Figure 3 The preference for the material demonstrated (y-axis) to the 24 observer pairs (x-axis). Each pair of bars represents one male. The colour of the bar represents the demonstrated colour (open bar, pink; filled bar, orange, which was the initially unpreferred material for each male). The hatched bar is the initial preference for the demonstrated material and the solid bar is the final preference for the demonstrated material. The dependent measure in the first preference test is the time observers spent interacting with tied-down string of two colours (pink and orange). Males then watched demonstrators build with 100 pieces of the observer's unpreferred material. The dependent measure in the final preference test was the proportion of pieces of string of the demonstrated material the observer male took to the nest cup. The subjects are arranged on the x-axis according to whether they decreased ($n = 7$) or increased ($n = 16$) or did not change ($n = 1$, the first male on the x-axis) their preference for the demonstrated material across the two preference tests.

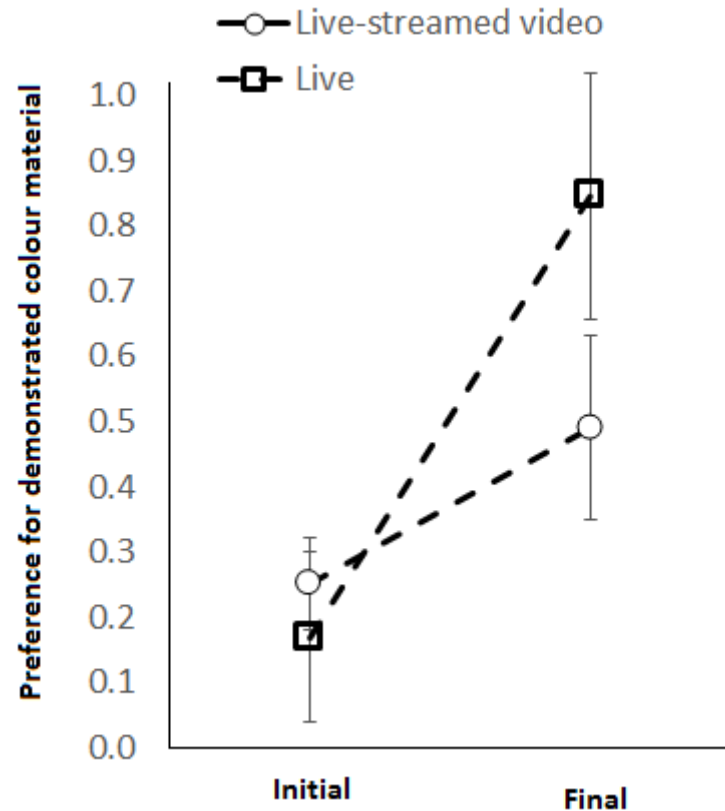


Figure 4 The initial and final preferences tests (x -axis) and the proportion of material of the demonstrated material (y -axis) for birds in the *Live-streamed video* experiment (open circles) and the birds from Guillette et al. (2016) in which observers watched live demonstrators, (*Live*, filled squares). Each symbol represents a group mean and the bars represent 95% confidence intervals. The dependent measure in the first preference test is the time observers spent interacting with tied-down string of two colours (pink and orange). Males then watched demonstrators build a nest with the observer's unpreferred material. The dependent measure in the final preference test was the proportion of demonstrated material brought to the nest cup by the observer male. These data, which include data that originally appeared in Guillette et al. (2016) are shown here according to CC BY 4.0 (creativecommons.org/licenses/by/4.0/).